

## Temporal and areal feeding behavior of the butterflyfish, *Chaetodon trifascialis*, at Johnston Atoll

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### Synopsis

The chevron butterflyfish, *Chaetodon trifascialis*, is found throughout the Indo-Pacific. It is a territorial, diurnal, corallivore found in close association with *Acropora* spp. corals. The feeding behavior of 33 individuals was studied over six seasons in three habitats. *Chaetodon trifascialis* spent one third of its active time feeding. However, there was much individual variation. Fish had significantly higher feeding rates during the early afternoon, and there were no significant differences in the feeding rates between the seasons. Feeding rates were significantly different between the three habitats. The *Montipora*-rich habitat had the highest feeding rates ( $\bar{x} = 10.74 \text{ bites min}^{-1} \pm 0.87$ , all corals combined) and the *Acropora*-*Montipora* mixed habitat had the lowest feeding rates ( $\bar{x} = 4.58 \text{ bites min}^{-1} \pm 0.63$ , all corals combined). Females fed significantly more than males. While *C. trifascialis* had been thought to only eat *Acropora* spp. corals, it occasionally fed on *Montipora* spp. and *Pocillopora* sp. corals when *Acropora* spp. were scarce. *Chaetodon trifascialis* exhibited patterns predicted by foraging theory of an energy maximizer. Territory sizes were inversely related to food density and feeding rates were inversely related to intruder rates. This is a promising system for future testing of foraging strategy models.

### Introduction

The butterflyfishes of the world (Perciformes, Chaetodontidae) exhibit a wide range of feeding behaviors, from planktivory to corallivory (Hiatt & Strasburg 1960, Talbot 1965, Hobson 1974, Reese 1975, 1977, 1981, Burgess 1978, Birkeland & Neu-decker 1981, Harmelin-Vivien 1981, Ralston 1981, Harmelin-Vivien & Bouchon-Navaro 1981, 1983). Though the feeding behaviors of some chaetodontids have recently been studied in detail (Gore 1984, Neu-decker 1985, Tricas 1986, Hourigan 1987), there are many species for which there is little information. One such species is *Chaetodon trifascialis* (*Megaprotodon trifascialis*).

*Chaetodon trifascialis* is found throughout the

Indo-Pacific, ranging from the Indian Ocean throughout Polynesia including the Northwest Hawaiian Islands. It does not, however, occur in the high Hawaiian Islands (Burgess 1978, Reese 1981). It is a territorial, diurnal, corallivore found in close association with *Acropora* spp. corals (Reese 1975). This butterflyfish has a specialized, forcep-like jaws which are well suited to removing single coral polyps (Motta 1985, 1988). *Chaetodon trifascialis* has been observed feeding almost exclusively on *Acropora* spp. corals (Reese 1975, 1977, 1981, Masuda et al. 1984). No other chaetodontid is known to be so specialized in terms of its prey choice.

*Chaetodon trifascialis* is solitary (Reese 1975, 1977) and site attached. Individuals have been ob-

served in the same territory for up to three years in this study and up to seven years at Enewetak Atoll (Reese 1981). It has been postulated that males and females hold adjacent territories (Reese 1973). However, the sexes are monomorphic and can not be distinguished in the field.

*Chaetodon trifascialis* is inactive at night, hiding in the coral. Fish become active at sunrise and remain active until sunset.

This study posed the following questions about the feeding behavior of *C. trifascialis*: 1. Are there differences in the feeding rates throughout the day or between seasons? 2. Are there differences in the feeding rates of males versus females? 3. Are there differences in the feeding rates of fish in different habitats? 4. Are there preferences for one species of coral or does the percentage of bites on a coral species correspond to its respective abundance? 5. How much time do the fish spend feeding in relation to other activities?

## Material and methods

### Study area

Johnston Atoll is located approximately 1250 km southwest of the Hawaiian Islands. It is approximately 17 km long and 5 km wide. An estimated 30–40% of the live coral cover in the lagoon area is composed of *Acropora cytherea* and the remaining 60% is mostly *Montipora verrucosa*, *M. patula*, and *M. verrilli* (Irons et al. 1984). Since *M. patula* and *M. verrilli* are virtually impossible to distinguish in the field, I will refer to these two species together as *M. patula/verrilli*.

### Coral cover

Data were collected in three separate habitats. The *Acropora*-rich habitat had approximately 90% of the live coral coverage consisting of *Acropora cytherea*. This habitat was located approximately 60 m inside the barrier reef at a depth of 7 m.

The *Acropora*-*Montipora* mixed habitat had about 75% coverage of *A. cytherea* and about 20%

*Montipora* spp. corals. This habitat was located 30 m off the east shore of Johnston Island at a depth of 3 m.

The *Montipora*-rich habitat had less than 1% *A. cytherea* and about 95% *Montipora* spp. corals. This habitat was located in the central lagoon at a depth of 10 m.

The percent coral cover at the *Acropora*-rich and the *Montipora*-rich habitats was calculated by placing five 1 m<sup>2</sup> quadrats randomly along a 100 m transect line. Four transect lines were layed parallel to each other and approximately 20 m apart in each habitat, making a total of twenty 1 m<sup>2</sup> quadrats for each of these two habitats. No transects were done in the *Acropora*-*Montipora* mixed habitat due to the topography.

### Identification

Individual fish were identified from natural variations of their markings (Reese 1973). Photographs of the left and right sides of each fish were taken to assist in the identification of individuals from one sampling period to the next.

### Feeding observations

Bites per coral species were counted for ten consecutive 5 min intervals, resulting in a total observation time of 50 min for each fish. A total of 76 50 min feeding periods were recorded for 33 fish. Data were collected in July 1984, January, April, August, October 1985, and January 1986. Four to seven fish in each of the three habitats were observed during each data collection trip. Certain fish, especially those in the *Acropora*-rich and the *Montipora*-rich habitats had as many as five feeding periods recorded, each in a different sampling period. At least two separate feeding periods were recorded for most individuals. Data were collected at all times of the day from sunrise to sunset.

All of the study individuals which remained in April 1986 were collected, except for three individuals which eluded capture. From time to time, individuals disappeared from their territories and

were not seen again, especially in the *Acropora-Montipora* mixed and the *Montipora*-rich habitats. Several of the focal individuals disappeared following a major storm which damaged portions of the study areas in February of 1986. The collected fish were sexed, weighed, and measured.

### *Territory sizes*

Each territory was roughly measured by recording its length and width. Territory sizes were estimated by the equation: Territory size = Length  $\times$  Width.

### *Statistics*

Each 50 min feeding period was tested for the randomness of the 5 min intervals comprising it using the runs test above and below the median (Sokal & Rohlf 1981). The sequence of 5 min intervals in only five of the 76 feeding periods significantly departed from randomness ( $p < 0.05$ ). As a result, each 5 min feeding interval was considered independent of the previous and following intervals. Data from these 5 min intervals were the smallest units of measurement used in the analyses. The data were collapsed by computing a mean of the 10 5 min intervals comprising each 50 min feeding period. These means were then used in the analysis of variances (ANOVAs) used in analyzing the data.

Separate two-way ANOVAs were used to test for differences between the seasons ( $S = 6$ ) and the hours of the day ( $D = 11$ ). Nested ANOVAs were used to test for differences between the habitats ( $H = 3$ ) and the sexes (male, female, and unknown). Individual fish ( $n = 33$ ) were used as the second factor in each two-way ANOVA and as the nested factor in each nested ANOVA to compensate for the repeated measures on each fish. Each two-way ANOVA and each nested ANOVA had a total of 76 cells. All analyses combined the sexes except for the nested ANOVA of the sexes and fish. Parametric pairwise comparisons were performed using Tukey's studentized range test (SAS 1985) and comparison limits were calculated to aid comparisons (Sokal & Rohlf 1981). All means re-

ported include plus or minus one standard error of the mean.

## **Results**

### *Are there differences in the feeding rates throughout the day or between seasons?*

There was substantial variation in the time spent feeding at the various hours of the day and at the different seasons (Fig. 1, 2). The high variation within and among the individuals made differences and trends in feeding rates throughout the hours of the day and between the seasons difficult to detect (Sokal & Rohlf 1981, Martin & Kraemer 1987).

Results from the two-way ANOVAs indicated significant differences between the hours of the day ( $p < 0.05$ ) and significant differences between fish ( $p < 0.05$ ) for both the feeding rates on all corals combined and the rates on *A. cytherea*. There were no significant differences between the seasons sampled ( $p > 0.35$ ) on both the rates on all corals combined and the rates on *A. cytherea*.

Tukey's studentized range test for the mean feeding rates through the hours of the day (Fig. 3) indicated that the fish fed significantly more ( $p < 0.05$ ) in the early afternoon than in the early morning and later afternoon.

### *Are there differences in the feeding rates of males versus females?*

Females had a significantly higher mean feeding rate ( $\bar{x} = 9.87 \text{ bites min}^{-1} \pm 0.58$ ,  $n = 9$ , all corals combined) than males ( $\bar{x} = 6.86 \text{ bites min}^{-1} \pm 0.89$ ,  $n = 8$ , all corals combined) for both the bites on all corals combined and the bites on *A. cytherea* alone (t-Test,  $p < 0.05$ ). There were no significant differences among females only and among males only (Tukey's studentized range test,  $p > 0.05$ ), except among the male feeding rates on *A. cytherea* alone (Tukey's studentized range test,  $p < 0.05$ ). However those differences were due mainly to two individuals.

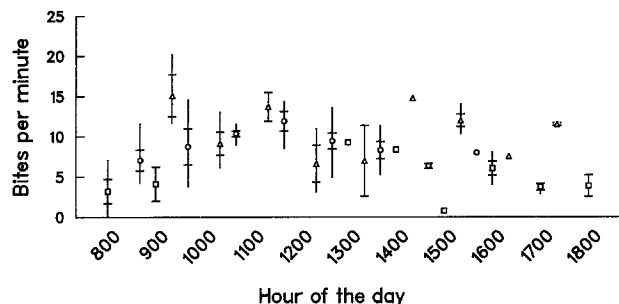


Fig. 1. Mean number of bites per minute  $\pm 1$  standard error and ranges on all coral types combined through the hours of the day. Not all habitats are represented for every hour of the day. The mean of each 50 min feeding period was used to calculate the hour means (total  $n = 76$ ). Points with no standard error or range represent the data from a single fish.  $\circ$  = *Acropora*-rich habitat,  $\square$  = *Acropora*-*Montipora* mixed habitat and  $\triangle$  = *Montipora*-rich habitat.

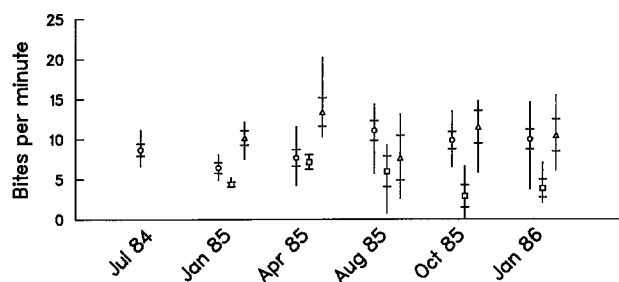


Fig. 2. Mean number of bites per minute  $\pm 1$  standard error and ranges on all coral types combined for the seasons sampled. The mean of each 50 min feeding period was used to calculate the season means (total  $n = 76$ ).  $\circ$  = *Acropora*-rich habitat,  $\square$  = *Acropora*-*Montipora* mixed habitat and  $\triangle$  = *Montipora*-rich habitat.

#### Are there differences in the feeding rates of fish in the three study habitats?

The feeding rates on all corals combined were significantly different between the three habitats. However, the mean feeding rate on *A. cytherea* in the *Acropora*-rich habitat ( $\bar{x} = 9.07$  bites  $\text{min}^{-1} \pm 0.48$ ,  $n = 36$ ) and the *Montipora*-rich habitat ( $\bar{x} = 8.88$  bites  $\text{min}^{-1} \pm 0.90$ ,  $n = 22$ ) were not significantly different from each other (Tukey's studentized range test,  $p > 0.05$ ). The feeding rates on *A. cytherea* at both the *Acropora*-rich and the *Montipora*-rich habitats were significantly higher than the

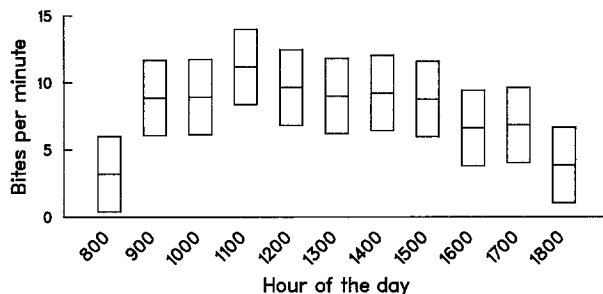


Fig. 3. Comparison limits of the mean feeding rates on all coral types combined through the hours of the day. Each box represents the mean feeding rate and its 95% comparison limits. Boxes which overlap are not significantly different from each other.

feeding rates in the *Acropora*-*Montipora* mixed habitat ( $\bar{x} = 4.56$  bites  $\text{min}^{-1} \pm 0.63$ ,  $n = 18$ , Tukey's studentized range test,  $p < 0.05$ ). Unexpectedly, the feeding rates on all corals combined of fish in the *Montipora*-rich habitat ( $\bar{x} = 10.74$  bites  $\text{min}^{-1} \pm 0.87$ ) tended to be higher than the feeding rates of fish in the *Acropora*-rich habitat ( $\bar{x} = 9.07$  bites  $\text{min}^{-1} \pm 0.48$ ).

#### Are there preferences for one species of coral or does the percentage of bites on a coral species correspond to its respective abundance?

The percentage of bites on each species of coral was very different than the abundance of the coral (Table 1). Results from the *Montipora*-rich habitat demonstrated *C. trifascialis*' strong preference for *A. cytherea*. Almost 83% of the total bites recorded in the *Montipora*-rich habitat were on *A. cytherea* which comprised less than 0.5% of the live coral in that habitat.

#### How much time do the fish spend feeding in relation to other activities?

Unlike other butterflyfishes (Tricas 1986, Hourigan 1987), *C. trifascialis* spent less than one-third of its active time feeding (Table 2). The major portion of its time was spent in patrolling (non-feeding activities, which included swimming around its ter-

ritory) and very little of its time was actually spent interacting (aggressive and non-aggressive behavior) with other fishes.

Individuals in the *Acropora*-*Montipora* mixed habitat spent much more time patrolling their territories (80%) than did individuals in the other two habitats. Interestingly, fish in the *Montipora*-rich habitat spent less time patrolling (62%) even though their territories were much larger than those of the fish in the other two habitats (Table 2).

## Discussion

*Chaetodon trifascialis* fed almost exclusively on corals of the Family Acroporidae (*Acropora* spp. and *Montipora* spp.). However, they fed on *Pocillopora meandrina* (Family Pocilloporidae) occasionally. Two *C. trifascialis* were also seen feeding on coral mucus in the water column. Suspended coral mucus was shown to contain a significant amount of organic matter and to be enriched with nitrogen when compared to more recently secreted coral mucus or microscopic particulate organic matter (Coles & Strathman 1973). This observation

suggests that *C. trifascialis* may be more flexible in its feeding behavior than previously thought.

Feeding rates varied during the day, but fish fed at a significantly higher rate in the early afternoon. Studies on *Acropora acuminata* indicate that lipid production is maximal during the early afternoon (Crossland et al. 1980). If a similar pattern holds for *A. cytherea*, *C. trifascialis* could be taking advantage of this increased lipid production by feeding more during this time of day.

There was no pattern to the differences in the feeding rates between the various seasons sampled. Intuitively, I would not expect any seasonal differences since water temperature at Johnston Atoll only varies within one degree Celsius during the year.

*C. trifascialis* is similar to other butterflyfishes in that males and females have different feeding rates (Tricas 1986, Hourigan 1987). Males and females do have adjacent territories and a single male has been observed interacting with up to three females. Males also seem to 'visit' females more than females 'visit' males. Chasing intruders and visiting females could prevent males from feeding as much as females. Also, since eggs are considered to be

Table 1. Percent of bites taken on each coral species (calculated as percent of the total bites taken within the respective habitat) and the coral composition of each habitat. Number in the brackets represents the percent of live coral.

Coral	<i>Acropora</i> -rich		Mixed		<i>Montipora</i> -rich	
<i>Acropora cytherea</i>	100	(91.90)	99.62	(75)	82.68	(0.32)
<i>Montipora patula/verrilli</i>	—	(1.25)	0.38	(8)	4.16	(51.02)
<i>M. verrucosa</i>	—		—	(12)	13.11	(44.46)
<i>Pocillopora meandrina</i>	—		—		0.04	(0.65)

Table 2. Time budgets of *C. trifascialis* in each habitat and relative territory sizes. Percentages represent the mean percent of active time spent performing the particular activity. Number in the brackets represents the standard deviation.

Activity	Combined data	<i>Acropora</i> -rich	Mixed	<i>Montipora</i> -rich
Feeding	29% (11)	30% (9)	16% (8)	36% (12)
Interactions				
Conspecifics	2% (1)	2% (1)	3% (1)	1% (<1)
Other species	<1% (<1)	<1% (<1)	<1% (<1)	<1% (<1)
Patrolling	68% (13)	68% (11)	80% (10)	62% (13)
Relative territory size (m <sup>2</sup> )		small <10	slightly larger <40	very large >400

more energetically costly than sperm (Trivers 1972), females should feed more than males.

*C. trifascialis* shows a definite preference for *A. cytherea* and correspondingly, territory sizes were inversely proportional to the density of *A. cytherea*. Fish in the habitat with a low density of *A. cytherea* tended to supplement their diet with some other coral species and spent more time feeding than did fish in the other habitats.

The mean feeding rate in the *Acropora-Montipora* mixed habitat was significantly lower than the rates in either of the other two habitats. The *Acropora-Montipora* mixed habitat had many schools of parrotfish, goatfish, jacks, and other butterflyfish species which often invaded individual's territories. The individuals in this habitat spent much more time patrolling their territories than the individuals in the other two habitats (Table 2).

Despite the fact that *C. trifascialis* spent only one-third of its active time feeding and two-thirds of its time patrolling its territory, this species could be classified as an energy maximizer. Foraging theory (Hixon 1980, Schoener 1983, 1987) predicts that if this species is indeed an energy maximizer, it should show the following patterns: 1. As food density increases, territory size decreases. 2. As intruder rate or defense time increases, feeding rate decreases. 3. As intruder rate increases, defense time increases. These are precisely the patterns observed in *C. trifascialis*. However, this system needs more study to test if indeed *C. trifascialis* is an energy maximizer, and what constraints, if any, would apply to this fish as an energy maximizer (Hixon 1980, 1982).

This system seems to be suitable for testing some of the foraging models proposed by Hixon (1980) and Schoener (1983, 1987). Future studies could provide insight into this system and the refinement of foraging strategy models and their predictions.

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